Aspects of the Life History and Population Biology of *Notospisula trigonella* (Bivalvia: Mactridae) from the Hawkesbury Estuary, Southeastern Australia

by

A. R. JONES AND A. MURRAY

Division of Invertebrates, The Australian Museum, P.O. Box A285, Sydney, 2000, Australia

AND

G. A. SKILLETER

School of Biological Sciences, University of Sydney, N.S.W. 2006, Australia

Abstract. Aspects of the life history of *Notospisula trigonella* and spatial and temporal variations in its abundance in the Hawkesbury Estuary, New South Wales, are described and related to physicochemical factors. Sexes were separate with a sex ratio close to 1:1. Spawning usually occurred between August and November but sometimes continued until February. Annual variation in the timing of onset and duration of spawning occurred and the nature of spawning cues is unclear. Recruitment always occurred between August and November, usually with a single cohort that appeared to survive about 1 yr. Growth rates were usually highest between November and February when cohorts of small size were present.

Spatial differences in abundance were usually significant but variable. The species was absent from salinities less than 10‰ and usually rare at sites closest to the ocean, where mean low-water salinities were 31.4‰. Water depth and sediment grade had little apparent effect on abundance as differences associated with the former were inconsistent and those with the latter were not significant. Temporal differences were somewhat cyclic in the middle estuarine reaches, with maximum abundance in November, but were variable in the lower reaches. Abundance fell to zero following a major flood. Much of the variability observed may ultimately be due to the unpredictable rainfall of the region.

INTRODUCTION

Notospisula trigonella (Lamarck, 1818) is a suspension-feeding mactrid bivalve found in estuaries and coastal waters of all Australian states (WILSON & KENDRICK, 1968). It inhabits a wide range of sedimentary habitats (ROBINSON & GIBBS, 1982) and can dominate the macrofaunal community with densities exceeding 2000 m⁻² (GREEN, 1968). Despite this, little is known about its life history and population biology. Available information is limited to a study of mortality (where it was called *N. parva*) by GREEN (1968), fragmentary notes in several benthic community studies (*e.g.,* CHALMER *et al.,* 1976; STEPHENSON *et al.,* 1977; RAINER & FITZHARDINGE, 1981; POORE, 1982) and STEJSKAL (1985).

This paper is based on information collected during a long-term study of the macrobenthic community of the Hawkesbury River estuary in southeastern Australia. Because it was the dominant species in the study, the biology of *Notospisula trigonella* is treated here separately from the rest of the fauna. The aims are to describe aspects of the life history (reproductive cycle, sex ratio, recruitment, and growth) and population biology (spatial and temporal distributions) in relation to physicochemical factors.

MATERIALS AND METHODS

Field Sampling

Twelve across-estuary transects containing 29 sampling sites were located between the mouth of the Hawkesbury

Table 1

Mean values for depth, mean grain size (M$_z$), % mud, and bottom-water salinity (adjusted to low-water values) for most sites over the first five samplings (summer 1977 to summer 1978 inclusive). The sites upstream of 9.1 and 9.2 included both deep and shallow sites on each transect and all had sediments with <20% mud. Salinities decreased from 7.3‰ at transect 10 to <0.5‰ at transect 14. Site 7A was 20 m deep with muddy sand sediments and salinity similar to site 7.1.

Site	Depth (m)	M$_z$ (ϕ)	Mud (%)	Salinity (‰)
1.1	4	6.0	59	31.4
1.3	10	4.4	31	31.4
2.1	4	6.1	61	29.7
2.2	5	6.0	60	29.7
2.3	12	7.7	88	29.7
3.1	12	5.4	49	27.9
3.2	6	3.1	17	27.9
3.3	5	8.1	93	27.9
6.2	8	4.4	36	24.0
6.3	8	1.7	6	24.0
7.1	12	5.7	51	20.5
7.2	8	2.1	13	20.5
7.3	6	7.6	83	20.5
8.1	6	6.0	57	16.8
8.2	16	3.4	17	16.8
9.1	20	6.2	63	11.8
9.2	6	3.0	20	11.8

Estuary and its junction with the Colo River (Figure 1). Sites on most transects varied in depth and sediment grade (Table 1). Samples were taken every season, with summer, autumn, winter, and spring being represented by February, May, August, and November respectively. All sites were sampled from February 1977 until February 1978 inclusive. Sampling was continued seasonally at sites 3.1 and 3.2 until spring (November) 1979 (*i.e.*, 3 yr total) and at sites 1.1, 1.3, 2.1, 2.2, 7.1, and 7.2 until summer (February) 1984 (*i.e.*, 7 yr total). No samples were taken at sites 1.3, 2.1, and 2.2 in autumn 1980 owing to equipment malfunction. Each sample comprised four 0.05-m^2 Smith-McIntyre grabs and material retained on a 1-mm sieve was preserved in buffered 10% formalin for subsequent laboratory processing under stereomicroscopes.

The salinity and temperature of bottom water were measured by a Goldberg temperature-compensated refractometer, a mercury thermometer (using water obtained by a closing water bottle), and a Martek Mark V *in situ* water quality analyzer whose sensors were lowered to the bottom. Sediment samples were taken from an additional grab taken at each time and site until autumn 1981. The sieve and pipette procedures of FOLK (1974) were used to analyze the grain size composition of the sand and silt-clay components respectively. River-discharge data were obtained from the New South Wales Metropolitan Water Sewerage and Drainage Board's gauging station at Penrith upstream of the tidal limit.

Life History

In summer 1980, a dense population was discovered at site 7A (Figure 1) from which one or two grabs were collected every three months until spring 1983. Specimens from this site were used to describe the reproductive cycle and estimate sex ratios, recruitment, and growth. The minimum reproductive size was determined for specimens from sites 7A, 7.1, 7.2, 2.1, and 3.1.

The interval between sampling (three months) is imposed by the logistics of a long-term community study and is greater than would normally be used for accurate descriptions of reproductive cycles. However, it is possible to gain considerable insight into the reproductive cycle by considering seasonal reproductive changes in conjunction with size-frequency distributions and by relating periods of spawning to those of recruitment (ROBERTS, 1984).

Fifteen individuals of 8 to 15 mm shell length were selected from each sample from site 7A and tissue specimens were prepared for histology. The gonadal portion of the visceral mass was removed and dehydrated in graded alcohols, cleared in xylene, embedded in paraffin wax, sectioned at 7-μm intervals, and stained with Harris' hematoxylin and eosin (CARLETON, 1957). At least 20 serial sections from each specimen were examined microscopically. Determination of the stage of gametogenesis was based on the classifications of BRALEY (1984) and ROPES (1968): *i.e.*, stage 0—resting or spent gonad; stage 1—early active; stage 2—late active; stage 3—ripe; stage 4—partially spawned; stage 5—spent. Allocation to a particular stage was made if more than 75% of the follicles showed this level of development.

Sex ratios and the minimum reproductive size were determined histologically and by observing the external condition (color) of the gonad in ripe individuals (stage 3). At other stages of gametogenesis, the color of the gonad could not be used to determine gender. In order to determine the minimum reproductive size, specimens ranging in size from 2 to 17 mm were examined for the presence of ripe gonad. Squash mounts of the gonad region of the visceral mass were used as a final check for small individuals without externally visible gonad.

Size Structure and Growth

Shell lengths of 200 randomly selected individuals from each sample taken at site 7A were measured with vernier calipers (±0.1 mm) and placed into 1-mm size classes. For samples with less than 200 specimens, all available individuals were measured. Estimates of mean cohort size from size-frequency distributions were made using normal probability paper (CASSIE, 1954). Growth rates were then estimated from the displacement of the mean length of those cohorts that were clearly recognizable and could be followed through time.

Figure 1

Map of Hawkesbury River estuary showing location of sampling sites. The transect number is indicated by the left hand numeral.

Data Analysis

Analyses of the relationship between the abundance of *Notospisula trigonella* and several abiotic variables (distance from the river mouth, water depth, sediment grade, season, year, river discharge, salinity, and temperature) were done. Some of these were confounded, *e.g.*, salinity varied with distance from the river mouth and sediment grade varied with both distance from the mouth and depth.

Differences in abundance associated with those variables whose levels could be fixed (distance from the river mouth, water depth, sediment grade, season, and year) were identified by analysis of variance (ANOVA) in various factorial combinations (see below) and *a posteriori* Student-Newman-Keuls (SNK) multiple comparisons. Cochran's test was used to test for variance heterogeneity and variance-stabilizing transformations were used where necessary. These ANOVAs deal with both spatial and temporal aspects of distribution and abundance.

Different spatial patterns during the first five sampling times were determined in the following ways. Patterns associated with distance from the mouth (along-estuary patterns) and depth (across-estuary patterns) arose from the transects containing both deep (>10 m) and shallow (3–6 m) sites. These data were analyzed by three-way fixed-factor ANOVAs (6 along-estuary positions × 2 depths × 5 times). Patterns associated with different sediments were identified by subjecting abundance data from transect 6 to a two-factor (sediment type × time) ANOVA. Only at transect 6 were sediment differences not confounded by depth differences. All the above ANOVAs included a time factor in order to assess the repeatability of various spatial differences in abundance.

Temporal patterns at transects with long-term data available (7 yr for transects 2 and 7) were analyzed by three-way fixed-factor ANOVAs (site × season × year). Year was considered a fixed factor because all available years were sampled. This fixed-factor model restricts inferences to the paricular sites, seasons, and years involved.

Relationships between abundance and those abiotic variables whose levels could not be fixed (temperature, salinity, and river discharge) were quantified using Spearman rank correlations and partial correlations. The latter provided statistical control for confounded variables, *i.e.*, the association between abundance and salinity (for example) could be quantified independently of the association with temperature and river discharge.

RESULTS

Physicochemical Characteristics of Sampling Sites

Considerable variation in physicochemical characteristics occurred. The mean salinity of bottom water varied from 31.4‰ at transect 1 to 11.8‰ at transect 9 (Table 1). No specimens of *Notospisula trigonella* were obtained in the lower salinities upstream of transect 9. There were temporal variations in salinity which were largely caused

by a major flood in March 1978, minor floods in March 1977 and June 1978, and a major drought from 1979 until 1981 (Figure 2). Recorded temperature of bottom water at site 7A varied from 25.7 to 14.4°C. The range was approximately 2°C greater and less in the upper (transects 11–14) and 2°C less in the lower (transects 1–3) reaches respectively. The finest and coarsest sediments were located in the lower and upper reaches respectively, and sediment grade varied substantially across the estuary at transects 3–9 (Table 1).

Sex Ratio and Minimum Reproductive Size

Notospisula trigonella has separate sexes and the population at site 7A displayed a sex ratio of 1:1.05 (male : female, $n = 240$) which is not significantly different from 1:1 ($\chi^2 = 0.15$, $P > 0.05$). No hermaphrodites were observed.

The minimum recorded shell length of reproductively mature individuals at site 7A was 5 mm. However, at sites 7.1, 7.2, 3.1, and 2.1, it was only 3–4 mm.

Spawning and Recruitment

Spawning, as indicated by the presence of partially spawned individuals, usually occurred in November and sometimes continued until February of the following year (Figures 3A–D). However, the timing of both the onset of spawning and its duration appeared to vary among years. For example, in 1981, partially spawned specimens (stage 4) were present in August, whereas in 1983 and 1982, this stage was not observed until November and the following February respectively (Figures 3B–D). Furthermore, spawning had probably concluded by February in 1981 and 1982 but was continuing during February of 1980 and 1983. In fact, the presence of spent individuals as late as May in 1980 implies an exceptionally long duration for the spawning period starting in 1979 (Figure 3A).

Recruitment of a new cohort always occurred between August and November but variability in the number of cohorts per year among years was apparent (Figure 4). In 1982 for example, cohort 4 had settled prior to the August sampling and was supplemented by cohort 5, which had settled prior to the November sampling (Figures 4K, L). Each cohort appeared to survive about 1 yr, except cohort 4, which suffered high early mortality (Figures 4L, M). Although spawning in 1980 and 1983 continued until February (Figures 3A, D), no recruitment ensued (Figures 4A–C, M–O), although specimens too small to be sampled may have settled temporarily.

Growth

In all years except 1982, growth rates showed a single peak between November and February. In 1982, growth rates peaked in this period and also between August and November when settlement (cohort 4) occurred earlier than
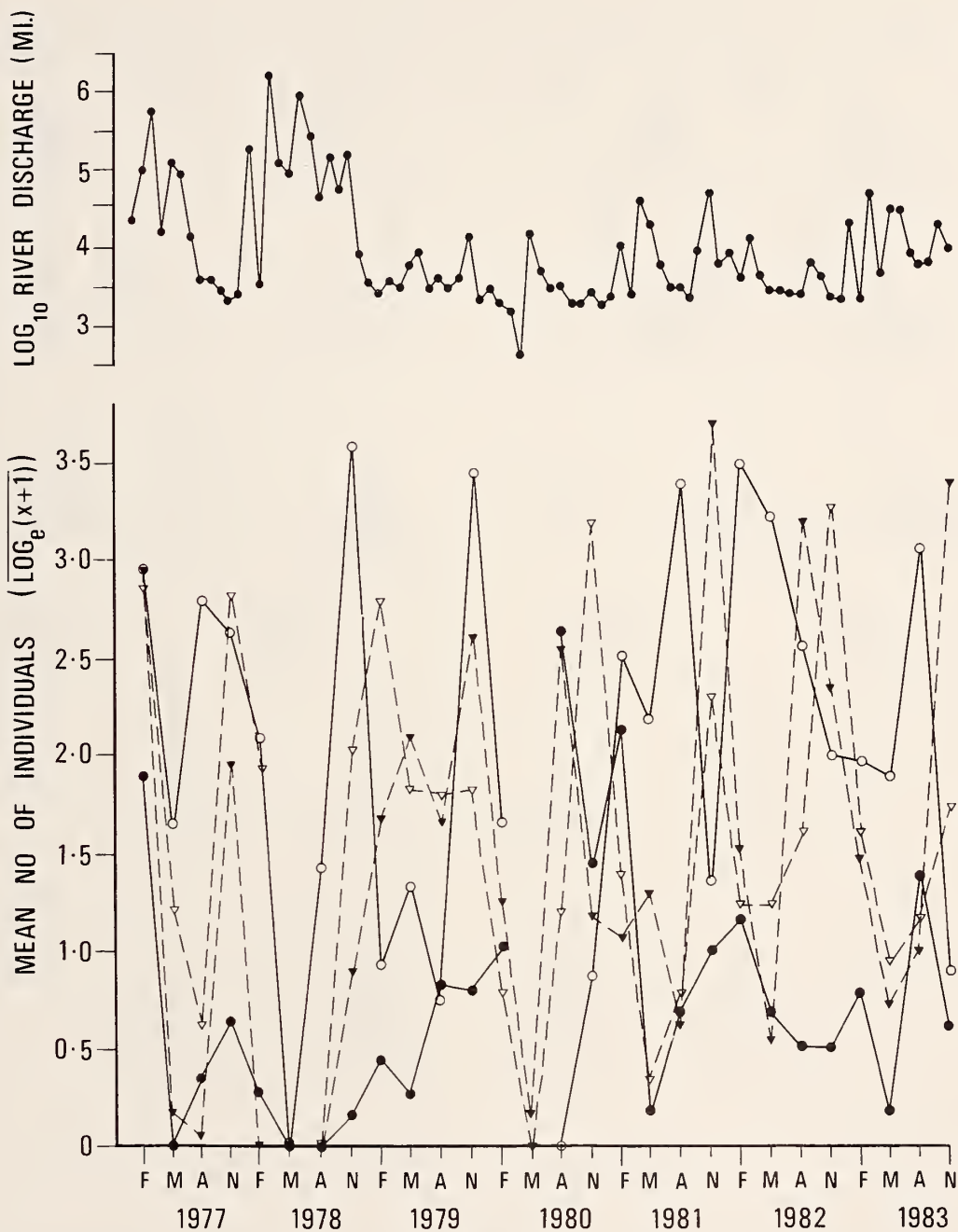
Figure 2

Temporal distribution (1977–1983 inclusive) of mean number of individuals per grab at sites 2.1 (●), 2.2 (○), 7.1 (▼), and 7.2 (▽). Standard errors are omitted for clarity but varied from 0.0 to 0.5 (2.1), 0.0 to 0.6 (2.2), 0.0 to 0.6 (7.1) and 0.0 to 0.8 (7.2) following data transformation to $\log_e(x + 1)$. $\log_{10}$ river discharge volumes are included. Ml = megalitres.

for other years. Growth for these three-month periods varied from 4.0 mm for cohort 2 in 1980–1981 to 10.5 mm for cohort 3 in 1981–1982 (Figure 4). In addition to varying seasonally, growth rates also varied with cohort

mean size. For example, the size of cohorts for all these high-growth periods was small, with mean shell lengths less than 5.6 mm. At other times, larger-sized cohorts (>8.4 mm mean length) were present and their growth
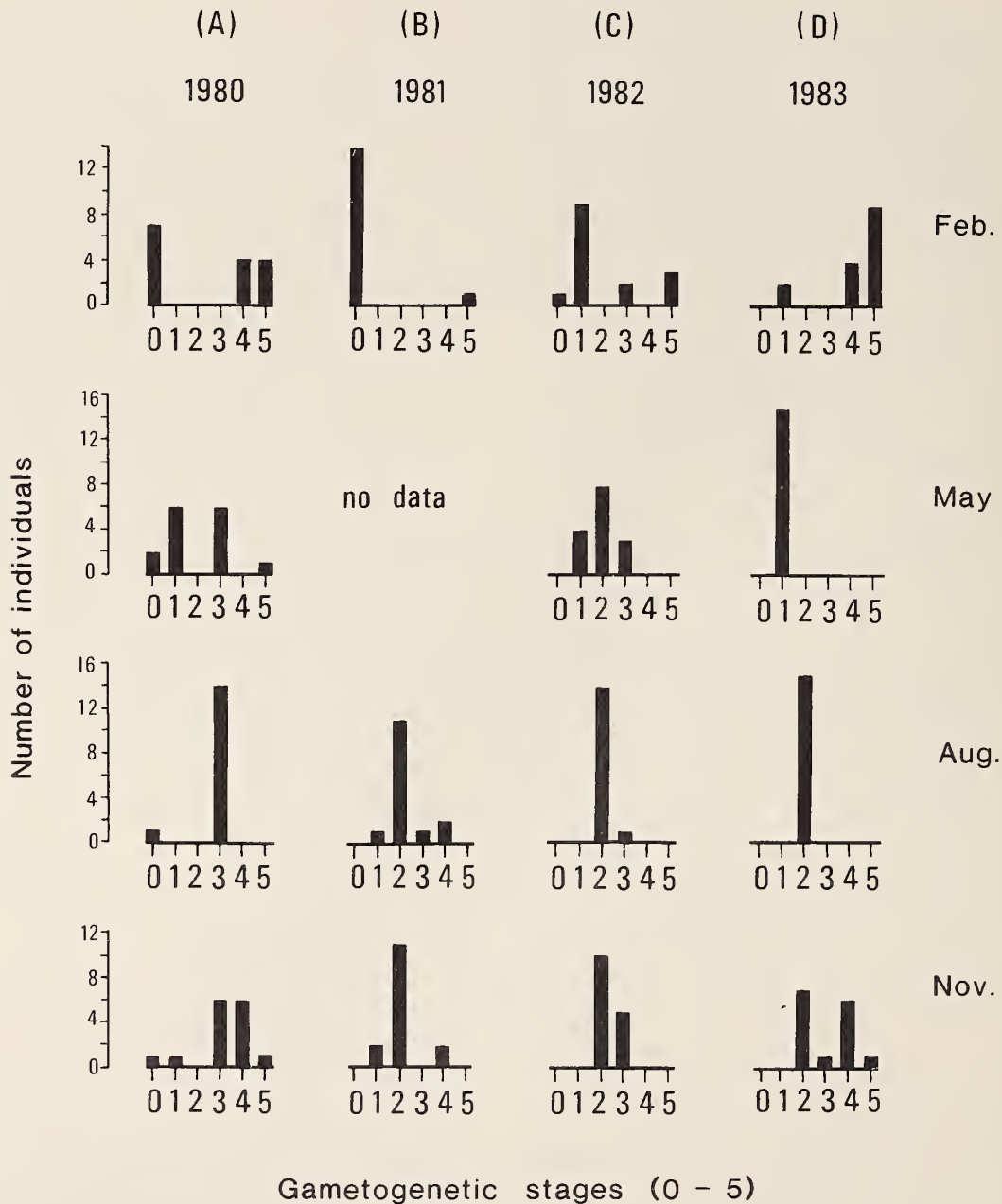
(A)   (B)   (C)   (D)

1980   1981   1982   1983

Number of individuals

Feb.

May

no data

Aug.

Nov.

Gametogenetic stages (0 - 5)

Figure 3

A–D. Temporal sequence of gametogenetic stages at site 7A from summer 1980 until spring 1983. The numbers 0 to 5 on the abscissa refer to gametogenetic stages with 0 = resting or spent gonad, 1 = early active, 2 = late active, 3 = ripe, 4 = partially spawned, and 5 = spent.

never exceeded 2.8 mm for any three-month period (Figure 4). Hence, the effect of season on growth rates was confounded by different sizes.

Growth rates also varied considerably among years. For example, growth for the November–February period of cohort 3 in 1981–1982 and cohort 5 in 1982–1983 was 10.5 mm and 4.8 mm respectively, even though the cohort mean size was identical (Figure 4).

Distribution and Abundance in Space and Time

Differences in abundance among transects, depths, and sediments, and with time, were often statistically significant. However, the patterns of difference were not consistent (ANOVA interaction terms significant) and, hence, any ecological importance of the main factors was obscured by complex interactions.
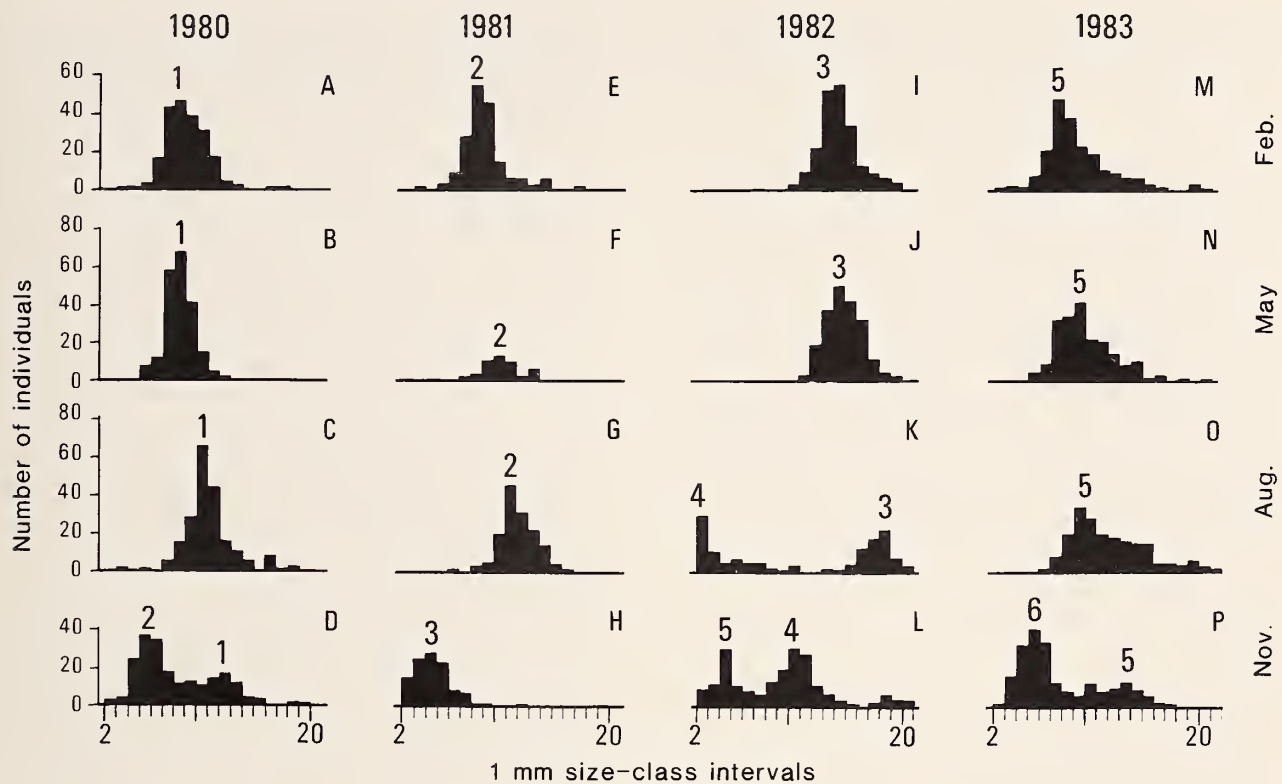
Figure 4

A–P. Size-frequency histograms for each sampling time at site 7A. $n = 200$ for all samples except F, G, H, and K where $n = 46, 145, 110,$ and 140 respectively. The cohorts are numbered 1–6.

Along-estuary patterns: The occurrence of *Notospisula trigonella* was restricted to the lower and middle reaches of the estuary, *i.e.*, transects 1–9 inclusive. Although significant differences in abundance among these transects usually occurred (three-way ANOVA, $F_{transect} = 243.2, P < 0.001$; SNK tests), the pattern varied with both depth and time (three-way ANOVA, all interaction terms significant). The species was absent or rare from both deep and shallow sites on transects 1 and 9. At deep sites, transects 2 and 3 were usually significantly richer than all other transects, while no consistent along-estuary pattern of difference emerged from shallow sites (SNK tests, Figure 5).

Across-estuary patterns: Depth-related differences in abundance occurred at all transects analyzed (three-way ANOVA, $F_{depth} = 640.2, P < 0.001$). However, the pattern of difference varied with time (*i.e.*, the richer site was sometimes shallow and sometimes deep; ANOVA interaction terms significant, SNK tests) everywhere except at transect 3. At transect 3, the deep site always yielded more specimens than the shallow site although this depth-related difference was confounded by sedimentary differences between the sites (Table 1).

At transect 6, sediments (but not water depth) varied between the two sites (Table 1). Differences in abundance between these sites were not significant during the first five sampling times (two-way ANOVA, $F_{site} = 4.1, P > 0.05$; $F_{interaction} = 2.2, P > 0.05$).

Temporal patterns: For the long-term (7-yr) data, significant seasonal and annual differences in abundance occurred at both transect 2 ($F_{season} = 12.1, P < 0.001$; $F_{year} = 8.9, P < 0.001$) and transect 7 ($F_{season} = 56.7, P < 0.001$; $F_{year} = 20.3, P < 0.001$). However, at both transects the seasonal patterns varied with both site and year and the yearly patterns varied with both site and season (three-way ANOVAs, second order interaction significant). Despite this significant interaction, patterns were relatively cyclic at transect 7, where peaks often occurred in November and low densities in May or August (Figure 2). However, abundance varied irregularly at transect 2. Following a major flood in March 1978, *Notospisula trigonella* was absent from all sites sampled in May 1978 and relatively rare in August 1978 (Figure 2).

Abundances at transects 2 and 7 were related to temporally changing physicochemical factors in the following ways. Spearman correlations between abundance and each of salinity and one-month river discharge were significant at sites 2.1, 7.1, and 7.2, but not at 2.2. Correlations with temperature were significant only at sites 2.1 and 7.2 (Table 2). Variation in these physicochemical factors never accounted for more than 22% of variation in abundance.
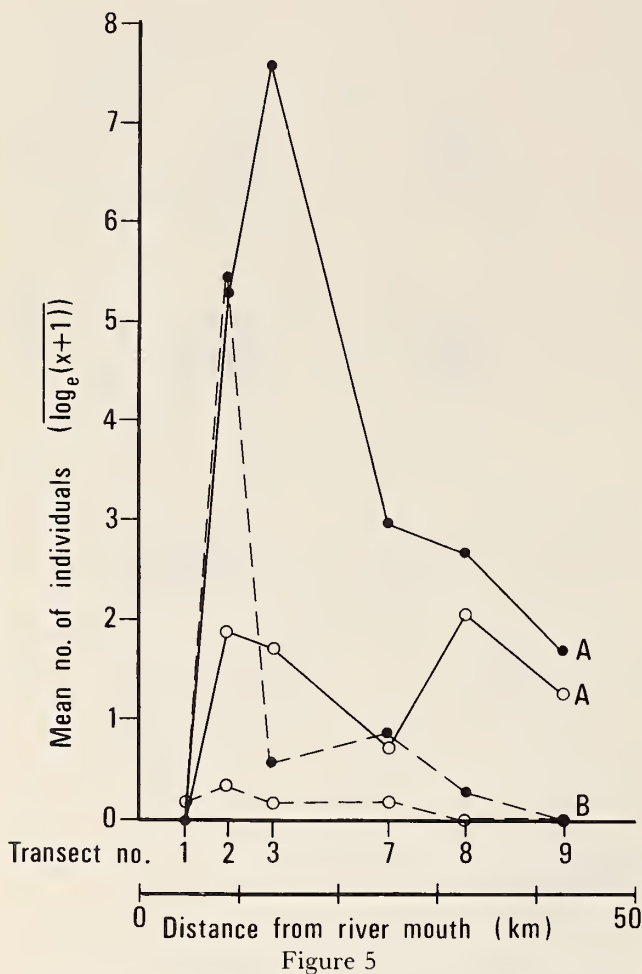
Figure 5

Along-estuary distribution of mean number of individuals per grab at shallow (O) and deep (●) sites for February 1977 (A) and August 1977 (B). Standard errors are omitted for clarity but varied from 0.0 to 0.5 (shallow, February), 0.0 to 0.5 (deep, February), 0.0 to 0.2 (shallow, August), and 0.0 to 0.4 (deep, August).

When the effects of two of the three physicochemical factors were held constant by second order partial correlation, only those correlations with salinity and temperature at site 7.2 were significant (Table 2).

DISCUSSION

Spawning and Recruitment

The appearance of a new cohort and the presence of partly spawned animals in November of most years (Figures 3, 4) indicate that spawning usually starts just prior to this month. This agrees with Hughes (personal communication) who found that specimens from the Swan Estuary in Western Australia first spawned in September–October. These findings suggest that rising temperature could be a spawning cue as found for other bivalve species (SASTRY, 1979). However, the variation in the onset and duration of spawning among years, despite similar temperature cycles, suggests that other factors could influence spawning.

Salinity changes can also cause spawning in some bivalve species (SASTRY, 1979) and spawning at low-flow (high-salinity) times would promote retention of planktonic larvae in the estuary. However, available evidence relating spawning in *Notospisula trigonella* with salinity changes are in conflict. For example, spawning occurred during increasing salinities in Western Australia (Hughes, personal communication) and apparently during decreasing salinities in Bramble Bay, Queensland (Stejskal, personal communication). Furthermore, partly spawned individuals were observed during both low- and high-flow conditions in the Hawkesbury Estuary. Hence, it appears that any role of salinity change as a spawning cue is either variable or else interacts with other factors.

Another feature of the life cycle of *Notospisula trigonella* is the relationship between spawning and recruitment. Although the length of the spawning period usually provided the opportunity for extended recruitment from November until February, only a single cohort appeared in most years

Table 2

Spearman (r_s) and partial (r_p) correlation coefficients between abundance of *Notospisula trigonella* and each physicochemical variable at sites (2.1, 2.2, 7.1, and 7.2) with 7 yr of data available. Partial correlations are second order, *i.e.*, both other physicochemical variables were controlled. *, **, *** = $P < 0.05$, 0.01, and 0.001 respectively, two-sided test.

Physicochemical variable		Site			
		2.1 ($n = 112$)	2.2 ($n = 113$)	7.1 ($n = 116$)	7.2 ($n = 115$)
Salinity	r_s	0.38***	−0.05	0.33***	0.46***
	r_p	0.12	0.15	0.12	0.23**
River discharge	r_s	−0.25**	0.03	−0.23**	−0.36***
	r_p	−0.17	0.15	0.03	−0.17
Temperature	r_s	0.25**	0.04	0.18	0.33***
	r_p	0.04	0.05	0.03	0.32***

(Figure 4), always early in the spawning season. Any settlement at other times did not yield specimens sufficiently large to be sampled. STEJSKAL (1985) also found recruitment in Bramble Bay, Queensland, restricted to single cohorts. In the present study, several factors may account for this pattern. For example, high river flows after November in some years (Figure 2) may have washed potential settlers downstream. Alternatively, the high densities present after settlement of the first cohort may impede further settlement through their suspension feeding on settling individuals (WOODIN, 1976). However, if this latter mechanism does apply, it was insufficient to prevent the settlement of two cohorts in 1982.

Growth

Growth rates varied seasonally, usually being highest between November and February. At this time, most specimens were small and, hence, the effects of season and size on growth rate were confounded. The decline in growth rate with size was probably caused by resources being diverted from somatic to gonadal growth following the onset of sexual maturity (CERRATO, 1980). However, other factors associated with changing seasons may also have influenced growth rates.

Growth rates also varied among years as shown by comparisons between cohorts of similar mean size from different years. From November 1981 to February 1982, the growth rate was the highest recorded and more than twice the rate for summer 1980–1981 and 1982–1983. This high-growth period coincided with increased river flows (but not of flood status) which may have enhanced the food supply, hence accounting for the high level of growth. Similarly, the growth rate for adults during spring (August to November) of 1983, which experienced high flows, was much greater than the growth rate of similar-sized animals in 1980 when flows were low. However, the relationship between growth and flow rate was non-monotonic, as abundance was low or zero following the floods of 1977 and 1978. Although few studies have related food availability and bivalve growth, WILDISH & KRISTMANSON (1985:237) showed that the growth of blue mussels "may be controlled by tidal current speed through its effect on seston supply." Further, JOSEFSON (1982) found that food supply rather than temperature affected the growth rate of *Abra alba*.

Growth rates of *Notospisula trigonella* also appear to vary with geographical location. For example, the Hawkesbury cohort 3 (Figures 4H–K) reached its maximum size (19 mm mean shell length) in nine months and may have persisted for only 12–15 months. By contrast, individuals of *N. trigonella* from Bramble Bay, Queensland, were only 14–16 mm long at an estimated age of 20–24 months (Stejskal, personal communication). Alternatively, the population at Bramble Bay may have grown more slowly because it was intertidal (and hence had less feeding time) rather than some geographical factor, or else because age estimates might have been in error.

Because of the limitations imposed by the low temporal resolution in sampling, the above life-history interpretations have provisional status only.

Distribution and Abundance

Spatial differences in abundance were not only usually statistically significant but also inconsistent. Such variability appears common both for *Notospisula trigonella* elsewhere (STEJSKAL, 1985) and for other bivalve species (O'FOIGHIL *et al.*, 1984; GIBBS, 1984). Although these inconsistent patterns make it difficult to suggest factors controlling abundance, available evidence suggests the upstream limit of *N. trigonella* may be influenced by salinity. Hughes (personal communication) found high mortality in laboratory populations held in salinities below 5‰, and both this study and that of POORE (1982) in the Gippsland Lakes failed to find this species below 10‰ in depths and sediment grades similar to populated sites of higher salinity.

Although no consistent downstream distributional limit was observed in the present study, *Notospisula trigonella* was absent or rare from transect 1 and also from the high-salinity sites near the mouth of the Gippsland Lakes (POORE, 1982). Furthermore, abundance in large marine bays can be enhanced near freshwater inputs (POORE & RAINER, 1974; STEJSKAL, 1985). These results suggest that marine salinities or some associated factor (see, *e.g.*, BOESCH, 1977) inhibit *N. trigonella*.

Significant across-estuary differences in abundance were sometimes associated with both depth and sediment grade. These patterns resemble those of other mactrid bivalve species (HOLLAND, 1985). However, neither depth nor sediment grade was useful for predicting abundance because the nature of the relationship varied with time, location, or both. Furthermore, at transect 6 where sediment changes were not confounded with depth, significant differences in abundance did not occur. These results suggest that sediment specificity is low in this species. Other studies have found *Notospisula trigonella* to occupy sediments ranging from mud (POORE & KUDENOV, 1978) to sand (MACPHERSON & GABRIEL, 1962; Hughes, personal communication). However, experimental work by Jones (personal communication) found that silt and fine sand attracted more specimens than coarse sand (which did not characterize any Hawkesbury site) where burrowing was difficult. Of course, factors such as hydrodynamic forces are confounded with water depth and sediment grade and may influence adult abundance through their effect on larval distribution or food supply.

Temporal Patterns

While temporal differences in abundance were often highly significant, the patterns of difference were very variable. For example, seasonal differences were not always repeatable over years. Some of this variation can be

explained by the occurrence of a major flood in March 1978 and a minor flood in March 1977 after which *Notospisula trigonella* was uniquely absent and rare respectively. Hence, the seasonal patterns of abundance were altered for these years.

Other estuarine invertebrate species also show substantial temporal variability (BOESCH *et al.*, 1976a; HOLLAND, 1985). One of these is the mactrid bivalve *Mulinia lateralis* which exhibits high fecundity, rapid growth, and early maturity (BOESCH *et al.*, 1976a). *Notospisula trigonella* shares some of these traits, which probably promote survival in a variable and disturbance-prone environment (GRASSLE & SANDERS, 1973).

In contrast, another estuarine mactrid bivalve, *Rangia cuneata,* has a life history that differs from the above species by having long life (at least 8 yr) and by being persistently present in samples taken between 1969 and 1975 (BOESCH *et al.*, 1976a). Temporal variability in abundance was also comparatively low. Consequently, attempts to generalize about estuarine life-history strategies, even among confamilial species, will fail. However, a partial explanation of these differing strategies arises from the following. Estuaries are far from uniform habitats, and species in different salinity zones often differ in their response to disturbance (BOESCH *et al.*, 1976b; Jones, in preparation). *Mulinia lateralis* and *Notospisula trigonella* both inhabit salinities exceeding 10‰ where flood-induced salinity depression, and hence the magnitude of disturbance, would be greater than for *R. cuneata*, which lives in salinities lower than 10‰. Unlike the other two mactrids, *R. cuneata* can survive severe flooding with the probable consequence of longer life and increased buffering of temporal fluctuations.

Although the decreased abundance of *Notospisula trigonella* associated with floods suggests that greatly decreased salinity lowers abundance, the effect of salinity is confounded with the sediment changes that accompany floods. Sediment erosion and deposition and turbidity can kill other bivalve species (PERKINS, 1974; PETERSON, 1985). Being a surface-dwelling suspension feeder with short siphons, *N. trigonella* would probably be particularly susceptible to these sediment changes, especially as Jones (personal communication) found sediment disturbance to affect significantly the abundance of this species.

Although some short-term changes can be explained by the effects of floods, factors such as salinity, river discharge, and temperature never explained more than 22% of the long-term variation (Table 2), a similar result to that obtained for *Mulinia lateralis* in the Chesapeake Bay (HOLLAND, 1985). Furthermore, most of the partial correlations concerning *Notospisula trigonella* were not significant. This high degree of unexplained variability is typical of the zoobenthos of the Hawkesbury Estuary, where rainfall is itself temporally unpredictable (Jones *et al.*, in preparation).

ACKNOWLEDGMENTS

LITERATURE CITED

BOESCH, D. F. 1977. A new look at the zonation of benthos along the estuarine gradient. Pp. 245–266. *In:* B. C. Coull (ed.), Ecology of marine benthos. Univ. South Carolina Press: Columbia.

BOESCH, D. F., R. J. DIAZ & R. W. VIRNSTEIN. 1976b. Effects of tropical storm Agnes on soft-bottom macrobenthic communities of the James and York Estuaries and the Lower Chesapeake Bay. Chesapeake Sci. 17:246–259.

BOESCH, D. F., M. L. WASS & R. W. VIRNSTEIN. 1976a. The dynamics of estuarine benthic communities. Pp. 177–196. *In:* M. Wiley (ed.), Estuarine processes. Vol. 1. Uses, stresses, and adaptation to the estuary. Academic Press: New York.

BRALEY, R. D. 1984. Mariculture potential of introduced oysters *Saccostrea cucullata tuberculata* and *Crassostrea echinata* and a histological study of the reproduction of *C. echinata.* Aust. Jour. Mar. Freshwater Res. 35:129–141.

CARLETON, H. M. 1957. Histological technique. 3rd ed. Chapter VII, pp. 93–100. Oxford University Press: London.

CASSIE, R. M. 1954. Some uses of probability paper in the analysis of size frequency distributions. Aust. Jour. Mar. Freshwater Res. 5:513–522.

CERRATO, R. M. 1980. Demographic analysis of bivalve populations. Pp. 417–465. *In:* D. C. Rhoads & R. A. Lutz (eds.), Skeletal growth of aquatic organisms: biological records of environmental change. Plenum Press: New York.

CHALMER, P. N., E. P. HODGKIN & G. W. KENDRICK. 1976. Benthic faunal changes in a seasonal estuary of South-western Australia. Rec. West. Aust. Mus. 4(4):383–410.

FOLK, R. L. 1974. Petrology of sedimentary rocks. Hemphill: Austin. 182 pp.

GIBBS, P. E. 1984. The population cycle of the bivalve *Abra tenuis* and its mode of reproduction. Jour. Mar. Biol. Assoc. U.K. 64:791–800.

GRASSLE, J. F. & H. L. SANDERS. 1973. Life histories and the role of disturbance. Deep-Sea Res. 20:643–659.

GREEN, R. H. 1968. Mortality and stability in a low diversity subtropical intertidal community. Ecology 49:848–854.

HOLLAND, A. F. 1985. Long-term variation of macrobenthos in a mesohaline region of Chesapeake Bay. Estuaries 8:93–113.

JOSEFSON, A. B. 1982. Regulation of population size growth and production of a deposit-feeding bivalve: a long-term field study of three deep-water populations off the Swedish coast. Jour. Exp. Mar. Biol. Ecol. 59:125–150.

MACPHERSON, J. H. & C. J. GABRIEL. 1962. Marine molluscs of Victoria. Melbourne University Press: Melbourne. 475 pp.

McLachlan, A. & T. Erasmus. 1974. Temperature tolerances and osmoregulation in some estuarine bivalves. Zool. Africana 9(1):1–13.

O'Foighil, D., D. McGrath, M. E. Conneely, B. F. Keegan & M. Costelloe. 1984. Population dynamics and reproduction of *Mysella bidentata* (Bivalvia: Galeommatacea) in Galway Bay, Irish west coast. Mar. Biol. 81:283–291.

Perkins, E. J. 1974. The biology of estuaries and coastal waters. Academic Press: London. 678 pp.

Peterson, C. H. 1985. Patterns of lagoonal bivalve mortality after heavy sedimentation and their paleoecological significance. Paleobiology 11:139–153.

Poore, G. C. B. 1982. Benthic communities of the Gippsland Lakes, Victoria. Aust. Jour. Mar. Freshwater Res. 33:901–915.

Poore, G. C. B. & J. D. Kudenov. 1978. Benthos of the Port of Melbourne: the Yarra River and Hobson's Bay, Victoria. Aust. Jour. Mar. Freshwater Res. 29:141–156.

Poore, G. C. B. & S. Rainer. 1974. Distribution and abundance of soft-bottom molluscs in Port Phillip Bay, Victoria, Australia. Aust. Jour. Mar. Freshwater Res. 25:371–411.

Rainer, S. F. & R. C. Fitzhardinge. 1981. Benthic communities in an estuary with periodic deoxygenation. Aust. Jour. Mar. Freshwater Res. 32:227–243.

Roberts, D. 1984. A comparative study of *Lasaea australis, Vulsella spongiarum, Pinna bicolor* and *Donacilla cuneata* (Mollusca; Bivalvia) from Princess Royal Harbour, Western Australia. Jour. Moll. Stud. 50:129–136.

Robinson, K. & P. Gibbs. 1982. A field guide to the common shelled molluscs of New South Wales estuaries. Coast and Wetlands Society: Sydney. 56 pp.

Ropes, J. W. 1968. Reproductive cycle of the surf clam, *Spisula solidissima,* in offshore New Jersey. Biol. Bull. 135:349–365.

Sastry, A. N. 1979. Pelecypoda (excluding Ostreidae). Chapter 5. *In:* A. C. Giese & J. S. Pearse (eds.), Reproduction of marine invertebrates. Vol. V. Molluscs: Pelecypods and lesser classes. Academic Press: New York.

Stejskal, I. 1985. The spatial and temporal patterns of the macrofauna of a subtropical muddy sandflat in southeast Queensland, Australia. Ph.D. Thesis, University of Queensland, Brisbane.

Stephenson, W., S. D. Cook & Y. I. Raphael. 1977. The effect of a major flood on the macrobenthos of Bramble Bay, Queensland. Mem. Queensl. Mus. 18:95–119.

Weinberg, J. R. 1985. Factors regulating population dynamics of the marine bivalve *Gemma gemma*: intraspecific competition and salinity. Mar. Biol. 86:173–182.

Wildish, D. J. & D. D. Kristmanson. 1985. Control of suspension feeding bivalve production by current speed. Helgolander wiss. Meeresunters 30:445–454.

Wilson, B. R. 1969. Survival and reproduction of the mussel *Xenostrobus securis* (Lamarck) (Mollusca; Bivalvia; Mytilidae) in a Western Australian estuary. Pt. II: Reproduction, growth and longevity. Jour. Natur. Hist. 3:93–120.

Wilson, B. R. & G. W. Kendrick. 1968. The recent appearance of *Notospisula parva* (Lamarck) (Mollusca; Bivalvia; Mactridae) in the Swan Estuary. Jour. Malacol. Soc. Aust. 1:25–31.

Woodin, S. A. 1976. Adult-larval interactions in dense faunal assemblages: patterns of abundance. Jour. Mar. Res. 34:25–41.